Community convergence and recruitment of keystone species as performance indicators of artificial reefs

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Title: Community convergence and recruitment of keystone species as performance indicators of artificial reefs

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Abstract

An experimental artificial reef was constructed in Strangford Lough, Northern Ireland as part of trials to regenerate damaged biogenic reefs formed by the horse mussel *Modiolus modiolus*. Experimental reef plots were constructed using *Pecten maximus* shell as cultch. Clumps of live adult *M. modiolus* were translocated from nearby natural reefs into cultch with a high profile (elevated cultch), cultch with a low profile (flattened cultch), as well as directly into the seafloor. The aim of the study was to test the hypothesis that translocated mussel clumps would increase habitat complexity thus accelerating community succession and enhancing natural recruitment of *M. modiolus* spat. These effects were predicted to be greater on elevated cultch due to greater protection from predators and increased accessibility to food resources. Within the artificial reef array the translocated clumps had a significant positive effect on recruitment compared to cultch without mussels with average densities of spat settled on the translocated *M. modiolus* clumps ranging from 100 to 200 individuals m^{-2} compared to 4 to 52 spat m^{-2} on cultch without mussels. Recruitment of *M. modiolus* spat was also significantly higher on translocated horse mussels when compared to natural reefs where densities of 8 - 36 spat m^{-2} were recorded. Reef elevation appeared to provide some degree of protection from predators but differences in translocated *M. modiolus* survival on the different elevation treatments were not significant. In total, 223 taxa were recorded 12 months after reef construction. The presence of translocated clumps of *M. modiolus* was the main driver of the increases in faunal diversity and species abundance. Application of objective criteria to assess the performance of artificial reefs suggested that translocation of *M. modiolus* clumps alone achieved most of the restoration objectives. Consequently this pilot study demonstrates a straightforward and realistic intervention technique that could be used to kick start the regeneration and expansion of impacted mussel and similar biogenic reefs elsewhere.

Keywords: Biogenic reef; *Modiolus modiolus*; Shellfish; Habitat restoration; Artificial reef; Community composition

1. Introduction

Biogenic reefs formed by bivalves provide a wide range of ecological services such as seston filtration, benthic-pelagic coupling, provision of feeding and structural habitat for mobile species and attachment surfaces for sessile species (Brumbaugh et al., 2007; Coen et al., 2007; Holt et al., 1998), as well as seabed stabilization (Jones, 1951; Rees, 2009). In addition, the complex three-dimensional structure characteristic of pristine reefs supports high biodiversity (Coen et al., 2007; Mann and Powell, 2007; Powers et al., 2009) which can range from 25 associated taxa to well over 300 (Borthagaray and Carranza, 2007; Cranfield, 2004; Kenchington et al., 2006; Koivisto and Westerbom, 2010; Ojeda and Dearborn, 1989; Rees et al., 2008; Sanderson et al., 2008). When such habitats are compromised these features and services are reduced or lost and may recover slowly or not at all without intervention. The most widely used shellfish restoration technique involves the construction of artificial reefs as a way to address not only habitat loss and recruitment limitation of the keystone species, but also 'to mimic some characteristics of a natural reef' (Jensen, 1997; OSPAR, 2009). Reefs in bivalve restoration projects usually consist of suitable substrate or 'cultch' used to construct an elevated three-dimensional structure (Nestlerode et al., 2007); brood stock of the keystone reef-forming species is often added to the reef (Brumbaugh and Coen, 2009). The complexity created by the added substrate increases survival of juveniles of the keystone species (Bartol and Mann, 1997; Bartol et al., 1999; Nozawa, 2008) and provides refuge for associated biota (Breitburg, 1999; Tolley and Volety, 2005). The elevation of the cultch is a key element of artificial reef design for oysters, significantly increasing their recruitment and survival (Schulte et al., 2009). Translocation of mature stocks increases the production of larvae to effectively kick-start a declining population by addressing recruitment limitations (Barnabé and Barnabé-Quet, 2000; Caddy and Defeo, 2003).

Modiolus modiolus is a long-lived mussel of circumboreal distribution (Anwar et al., 1990; Rees, 2009) that also aggregates to form reefs that increase seabed stability (Jones et al., 1997; Meadows and Shand, 1989), biodeposition and habitat heterogeneity. The biodeposits constitute a microhabitat for a rich array of infaunal species that live and feed in them (Navarro and Thompson, 1997; Ojeda and Dearborn, 1989; Rees et al., 2008). Reef forming mussels (*M. modiolus*, *Mytilus*

edulis) also offer protection from predators (Koivisto and Westerbom, 2010; Lintas and Seed, 1994; Witman, 1985) and suitable substrata for sessile epifauna which, along with the infauna and crevice fauna, results in a very rich faunal assemblage (Erwin, 1977; Rees et al., 2008; Sanderson et al., 2008; Wildish et al., 1998) with some of the species exclusively linked to the reefs (Ojeda and Dearborn, 1989). Fish species are also known to use *M. modiolus* reefs for food and refuge (Rees, 2009; Roberts et al., 2011).

M. modiolus reefs were historically widespread throughout Strangford Lough, Northern Ireland (Brown and Seed, 1976; Erwin, 1977; Roberts, 1975) and were a major feature in its designation as a candidate Special Area of Conservation (SAC) and proposed Marine Protected Area (MPA). In the 1990s the reefs were reported to be in an 'unfavourable conservation status' because they had experienced a reduction in both condition and extent due to fishing impacts (Service and Magorrian, 1997; Magorrian and Service, 1998; Roberts et al., 2011; Strain et al., 2012).

This study assesses the potential for *M. modiolus* restoration using artificial reefs. The rationale for the reef design was based on (1) the wide use of cultch in restoration of biogenic reefs of the American oyster *Crassostrea virginica* (Barnes et al., 2010; Mann and Evans, 2004; Piazza et al., 2005); (2) reports that *M. modiolus* recruitment occurs primarily amongst the byssal threads of adult conspecifics (Rees et al., 2008); and (3) that recruit survival in reef-forming bivalves such as *C. virginica* increases with reef elevation (Lenihan, 1999; Powers et al., 2009; Schulte et al., 2009). The experimental *M. modiolus* reef system was constructed using a total 16 tonnes of scallop shell distributed in replicated plots with different elevations. More than 6000 adult *M. modiolus* were collected from impacted patches of mussels close to the artificial reef and translocated into elevated and flattened cultch as well as seafloor plots. The key objective of this experimental reef array was to pilot different reef designs which might subsequently be scaled up in a more extensive restoration exercise.

This paper describes the results of a comprehensive survey carried out 12 months after construction of the artificial reef. The main aim of the survey was to determine whether translocation of the keystone species, *M. modiolus*, into an artificial reef constructed from shell cultch is an effective short-term strategy to stimulate recovery of damaged biogenic reefs. The performance of the reef 12 months after deployment

was assessed using criteria developed by Baine (2001) and by testing the following hypotheses: (1) communities would be more diverse in translocated mussels than on cultch or seafloor alone; (2) recruitment of *M. modiolus* spat would be greater on translocated mussel clumps than on cultch alone; (3) survival of *M. modiolus* translocated in clumps would be greater on cultch than directly on seafloor; and (4) recruitment and survival would be higher in mussels translocated onto elevated cultch than on other treatments. It was also predicted that communities associated with the artificial reef would become more diverse and would converge with adjacent natural *M. modiolus* biotopes over time.

2. Methods

2.1. Study area

The experimental reef was located in Strangford Lough, a large sea inlet on the east coast of Northern Ireland (Fig. 1) lying between 54° 35’ N and 54° 20’ N and between 5° 41’ W and 5° 34’ W. The Lough is 30 km in length and 8 km wide and occupies a total area of 150 km^2 (Service et al., 1996). Strangford Lough is a semi-enclosed sea lough connected to the Irish Sea by a narrow channel where the maximum depths (~60 metres) have been recorded and where tidal currents reach 4 m s^{-1}. The waters in the southern basin mix freely with the Irish Sea while the northern part of the lough is characterised by shallower depths and higher water retention times (Boyd, 1973; Ferreira et al., 2007). The markedly different hydrographical regimes found in different parts of the lough together with its glacial origin have created a wide range of habitats supporting a high diversity of marine communities with more than 2000 recorded species (Williams, 1953).

2.2. Ecological importance

Strangford Lough was designated as Northern Ireland's first Marine Nature Reserve and has been identified as a pilot Marine Protected Area (MPA) (Cork et al., 2006). It is also listed as a NATURA 2000 area [UK0016618] (JNCC, 2012). A key feature in this designation is the presence of biogenic reefs including *M. modiolus* reefs (DOENI, 1994; Roberts et al., 2011).

2.3. Artificial reef site selection

Site selection was carried out following published guidelines on selection of suitable sites for shellfish restoration (Brumbaugh et al., 2006; Caddy and Defeo, 2003; OSPAR, 1999). The reef should ideally be located in an area where: (1) targeted shellfish populations historically existed; (2) bottom conditions are adequate for supporting shell or other materials used; (3) natural recruitment is likely to occur; (4) the current velocity is likely to provide a good influx of nutrients and oxygen; and (5) it is protected from human activities. The artificial reef was established in the western side of Strangford Lough, ca. 1 km south of Brown Rocks (54° 25' 16" N, 5° 37' 13" W) and 17 m below chart datum (Fig. 1), an area of *Modiolus* shell and mud (Roberts et al., 2004) within the historical range of *M. modiolus* habitats in Strangford Lough (Erwin, 1977; Roberts et al., 2011). The reef was set up in an area designated to become a sea fisheries exclusion zone which was subsequently established in March 2011 by the Department of Agriculture and Rural Development of Northern Ireland (The Strangford Lough [Sea Fisheries Exclusion Zones] Regulations (Northern Ireland) 2011, SR2011/35). At this site currents are up to 62 cm s^{-1} at spring tides (unpublished data) and salinity was a little over 34 PSU while bottom temperatures ranged from 5 °C in January to 15 °C in July 2010. Average values for chlorophyll-a in the lough's south basin ranged from 0.345 to 5.19 µg l^{-1} for the duration of the monitoring period (data supplied by the Northern Ireland Environment Agency (NIEA)). In addition, *M. modiolus* spatfall has previously been recorded on mussel beds close to the experimental reef (unpublished data). Site assessments were made and licences obtained for the work in line with the relevant legal frameworks (Sayer and Wilding, 2005).

2.4. Artificial reef design and construction

The artificial reef array was constructed using ca. 16 tonnes of flat valves of the king scallop *Pecten maximus*. The shells were locally sourced from a scallop processing plant and weathered onshore for six months to avoid the introduction of undesirable

invasive species to Strangford Lough (Bushek et al., 2004). The shells were bagged in 0.5 and 1 tonne polypropylene bags prior to deployment.

A lifting crane positioned on a barge was used to lower the bagged cultch onto four random positions around a concrete block previously deployed to mark the centre of the licensed area. Each position contained four tonnes of bagged cultch divided equally into two sets to simulate elevated and flattened reefs. Once the arrangement was completed divers constructed four replicated flattened cultch plots by slashing one set of bags in each position and spreading the cultch to create an artificial reef of ca. 0.5 m elevation above the seafloor. The remaining untouched bags rose approximately 1 m above the seafloor serving as elevated cultch plots comparable to those used in oyster-restoration reefs constructed in North Carolina, USA (Lenihan, 1999). Finally, divers translocated 500 clumped horse mussels onto each treatment (four elevated and four flattened cultch plots) and also translocated 500 clumped horse mussels onto four areas of seafloor naturally devoid of *M. modiolus*. The translocated mussels only occupied a small proportion of the artificial reef array (approximately 1.6 to 2.4 m^2 out of 4 and 8 m^2 respectively occupied by each replicated elevated and flattened plot). The artificial reef array also included areas of elevated and flattened cultch as well as areas of uncultched seafloor without translocated mussels. In summary, the experimental reef array comprised a three by two crossed design, the factors being (1) elevation (elevated cultch, flattened cultch and seafloor) and (2) translocated *Modiolus* clumps (present, absent), with four replicates of each treatment (Fig. 2). The mussels (ca. 6000) used for translocation were collected by hand from *M. modiolus* beds located in close proximity to the artificial site and transferred to a laboratory where they were carefully separated to remove interstitial and sessile fauna. The mussels were transferred to holding tanks fed by a continuous flow of unfiltered seawater and allowed to clump for one month before translocation. To minimise crab predation, only mussels over 50 mm in length (Roberts, 1975) were translocated.

2.5. Reef monitoring program

2.5.1. Community composition and M. modiolus *spat recruitment on different reef types 12 months after construction*

Community composition was determined in March 2011, 12 months after construction of the artificial reef. The survey aimed to test the hypotheses that communities on elevated cultch, flattened cultch and the seafloor would differ and that communities would be more diverse on treatments that included translocated *M. modiolus*. Following the three by two crossed experimental design with four replicated plots described in Section 2.4, one 0.25 x 0.25 m quadrat was randomly placed on each of the 24 available areas (four replicates of each of six treatments; Fig. 2). All contents within the quadrat including *M. modiolus* clumps and cultch shell and sediment down to 10 cm were collected using a shovel and placed into 1 mm mesh bags. On return to the laboratory the bag contents including mussel clumps, cultch shells and sediment were washed through a 1 mm mesh size sieve and the retained fraction transferred to 4% formalin solution for 24 h tissue fixation. Following fixation, the sieved samples were washed onto a sorting tray and all the infaunal taxa collected with forceps under a dissecting microscope. The cultch shells and *M. modiolus* clumps were investigated separately for epifauna and crevice fauna including *M. modiolus* spat. All taxa collected were preserved in 70% ethanol and later identified at least to genus level and counted. Non-encrusting colonial epibiota were counted as clumps (sponges, tunicates) or branches (hydroids). Encrusting taxa such as sponges and bryozoans were identified and recorded as present.

2.5.2. Survival of translocated M. modiolus

A 0.25 m^2 quadrat was randomly placed by divers on translocated mussels on each of the 12 relevant plots: three elevation treatments (elevated cultch, flattened cultch, and seafloor) with translocated *Modiolus* clumps, four replicates. One diver placed the quadrat while the other diver remained stationary 0.5 m above it and recorded a 20 s videoclip using a HDV1080i high definition video camera (HDR7®, SONY Corporation) in an AMPHIBICO® housing equipped with two IKELITE® strobes. Once

the footage had been taken the second diver counted the numbers of live and dead *M. modiolus* to quantify the effect of different treatments on translocated horse mussel survival. The video footage was analysed on return to the laboratory and the number of live and dead mussels checked against the in-situ counts.

2.5.3. Comparison of communities on translocated mussels on the artificial reef with natural M. modiolus *communities*

To assess the artificial reef performance after one year's deployment, faunal assemblages associated with the three treatments that involved translocated clumps of *M. modiolus* were compared with natural *M. modiolus* communities from two adjacent, horse mussel reefs sampled in December 2010 using the same sampling methodology described in section 2.5.1 (Roberts et al., 2011). Remnant, relatively undamaged natural *M. modiolus* reefs in Strangford Lough are fragmented biogenic structures formed by infaunal and semi-infaunal horse mussel clumps rising up to 50 cm above the seafloor (personal observations). These *M. modiolus* populations were given the names of the closest geographical features as identifiers: Brown Rocks (BR) and Round Island Pinnacle (RIP) (54° 25' 42" N, 5° 35' 1" W and 54° 26' 4" N, 5° 35' 13" W respectively, Figs. 1 and 2).

2.6. Data analysis

2.6.1. Artificial reef faunal assemblage

Data matrices of all the faunal taxa identified from the video and removal quadrats and their abundances were compiled for statistical analysis using only specimens identified to at least genus level. Univariate and multivariate analyses were carried out to investigate infaunal and epifaunal community composition 12 months after construction and convergence with natural horse mussel reefs. Both univariate and multivariate analyses were undertaken using the PRIMER 6® software program (Clarke and Gorley, 2006) with the PERMANOVA + extension (Anderson et al., 2008). Univariate data manipulation and statistical comparisons were carried out using the open source software R (R Development Core Team, 2011).

2.6.1.1. Univariate analysis

The DIVERSE function (PRIMER) was used to calculate: Abundance of individuals (*N*), Margalef's species richness index (*d*), Shannon-Wiener diversity index (*H'*) and Pielou's Evenness index (*J*). All raw faunal data were checked for normality and homogeneity of variances using the Lillieford (Kolmogorov-Smirnoff) test and the Barlett's test respectively prior to undertaking parametric statistical analyses. If the conditions of normality and homocedasticity were met, two-way ANOVA models were fitted to identify significant effects of reef design and horse mussel translocation. All tests of null hypotheses were evaluated against a standard of $\alpha = 0.05$. A *post hoc* analysis (Tukey HSD test) was carried out where results were significant. Comparisons between univariate analysis results were displayed using boxplots constructed with the R package *ggplot2* (Wickham, 2009).

2.6.1.2. Multivariate analysis

All data were fourth root/log(x+1) transformed to down-weigh extremely abundant species such as *Pisidia longicornis*, *Pododesmus* spp. and *Ascidiella aspers*a. A similarity matrix was constructed using the Bray-Curtis similarity coefficient with the aim of identifying natural groupings amongst samples from different treatments. The matrix was subjected to a non-metric multidimensional scaling (MDS) algorithm using the default Kruskal fit scheme (Kruskal and Wish, 1978). The purpose is to represent the samples as points in a two- or three-dimensional scale, the distances between the different points being in the same rank order as the dissimilarities calculated by the Bray-Curtis coefficient. To assess whether differences in community composition between the different treatments were significant, Permutational MANOVA (PERMANOVA) fixed models (Anderson et al., 2008) were used as follows.

(1) Community composition associated with elevation and translocation 12 months post construction, two factors: (a) elevation, three levels = elevated cultch, flattened cultch, seafloor; and (b) translocation of *Modiolus* clumps, two levels = present, absent.

(2) Community convergence, one factor: reef type, two levels = natural *M. modiolus* reef and translocated *M. modiolus* (on either cultch or seafloor). The PERMANOVA analysis used the Bray-Curtis similarity matrix calculated after fourth root

transforming the raw abundance data. If significant differences between the assemblages were found a SIMPER analysis using PRIMER was carried out to identify the species that typified a group and which species accounted for the dissimilarities between groups. The initial tables of the SIMPER analysis list the typical taxa (found in consistently high abundances) in each group while pair-wise comparisons of species contribution are also given, indicating where the differences in faunal assemblage composition lay for each community sampled. *K*-dominance curves (Clarke, 1990) were also fitted to compare the artificial and natural reef communities. These plots display the cumulative abundance proportion against the log species rank. A more elevated curve represents less diverse assemblages while a curve that peaks slowly has higher numbers of species and more evenness (Lambshead, 1983)

2.6.2. Survival of translocated mussels and recruitment

Translocated *M. modiolus* mortality was defined as the number of empty valves divided by two. To offset the unequal relaying densities in each treatment the recorded mortalities were expressed as frequencies relative to the sum of live and dead mussels in each quadrat. Subsequently, the data were fitted to a linear model and a one-way ANOVA was carried out to investigate whether variation in translocated mussel mortality was explained by reef elevation. Variation in *M. modiolus* spat numbers between the reef elevation (elevated cultch, flattened cultch and seafloor) and translocation treatments (*M. modiolus* absent and present) was also investigated by means of a two-way ANOVA. Recruitment and mortality rates were checked for normality and heterocedasticity prior to carrying out all linear regression analysis. The statistical analyses were undertaken using the library stats in the R environment (R Development Core Team, 2011) while model assumptions were investigated with the R package *nortest* (Gross, n.d.). Additionally, boxplots summarizing the survival and recruitment data for each treatment were constructed with the R package *ggplot2* (Wickham, 2009).

3. Results

3.1. Community composition and M. modiolus *spat recruitment on different reef types 12 months after construction*

3.1.1. Community composition

3.1.1.1 Univariate analysis

Pooled data from the survey included 223 species belonging to 10 phyla (Supplementary data: Appendix A). Samples from translocated *Modiolus* clumps had pooled totals of 193 species compared to samples from flattened or elevated cultch without translocated *M. modiolus* clumps (105 species) and the unmodified seafloor (64 species). Communities across all treatments were dominated by polychaetes (33%), molluscs (31%) and crustaceans (28%) particularly encrusting species (*Pomatoceros lamarckii*, *P. triqueter, Pododesmus* spp. and *Balanus balanus*) (Table 1).

The assemblage associated with translocated *M. modiolus* clumps was very heterogeneous comprising 29% epifaunal (e.g. *Pomatoceros* spp., *Pododesmus* spp. and *B. balanus*), 51%,crevice (e.g. *Lysianassa ceratina*, *Pisidia longicornis*, *M. modiolus, Hiatella arctica*, *Kefersteinia cirrata* and *Cymodoce truncata*) and 21% infaunal species (e.g. *Aonides oxycephala*, *Mysella bidentata*, *Abra alba* and *Nucula nucleus*).The rare (Chapman et al., 2012) Connemara clingfish *Lepadogaster candoleii* was also recorded in the *M. modiolus* clumps.

Encrusting epifaunal taxa accounted for 81% of the total faunal abundance on areas of scallop cultch devoid of *M. modiolus*. The remaining 19% included non-encrusting epifauna, interstitial and vagile species, such as *Ascidiella aspersa, P. longicornis* and *Ophiothrix fragilis*.

The faunal assemblage at the treatment which can best be considered as a control (seafloor without translocated *M. modiolus* clumps) was typical of mixed mud and shell similar to a damaged ‘Sparse *Modiolus modiolus*, dense *Cerianthus lloydii* and

burrowing holothurians on sheltered circalittoral stones and mixed sediment' (SS.SMx.CMx.ClloModHo) or 'Infralittoral mixed sediment' (SS.IMX) biotopes (Connor et al., 2004; Roberts et al., 2004). The 10 most abundant taxa represented 57% of the community and included three epifaunal (*B. balanus, P. lamarckii* and *Pododesmus* spp.) attached to empty *M. modiolus* and *Chlamys varia* valves, four infaunal (*Nucula nucleus*, *Praxilella affinis*, *Paradoneis lyra* and *Owenia fusiformis*) and four crevice dwelling species (*Terebellides stroemi, P. longicornis, Lumbrineris gracilis and Orchomene nana*).

The communities associated with mussel clumps had significantly higher species diversity (*H'*) and richness (*d*) and evenness (*J*) than those treatments without translocation. However, total numbers of individuals (*N*) were very similar between reef array treatments with and without translocated *M. modiolus* clumps and not significantly different (Fig. 3; Table 2).
As regards to the effect of elevation there were no significant differences in species richness (*d*) between elevated cultch, flattened cultch and seafloor, while total numbers of individuals (*N*), species diversity (*H'*) and evenness (*J*) differed significantly between them (Fig. 3; Table 2).

Tukey HSD pair-wise comparisons confirmed reef elevation had no significant effect on the univariate indexes associated with translocated *M. modiolus* as the differences were significant only between elevation treatments without translocated mussel clumps. Numbers of individuals (*N*) in communities without translocated clumps were significantly higher in elevated and flattened cultch treatments compared to the seafloor ($P < 0.01$; $P < 0.05$). The *post hoc* analysis for differences between communities without translocated *M. modiolus* showed species diversity (*H'*) and evenness (*J*) were significantly higher on the seafloor relative to elevated (*H'*: $P < 0.001$; *J*: $P < 0.001$) and flattened (*H'*: $P < 0.001$; *J*: $P < 0.001$) cultch treatments and similar to those obtained for treatments with translocated *M. modiolus* clumps ($P > 0.05$, n.s.). The control plots (seafloor without translocated mussels) were characterised by poorer communities compared to all translocation treatments, based on lower numbers of individuals (*N*) and species richness (*d*). Nonetheless, these differences were not significant (Tukey's *post hoc* test: $P > 0.05$).

3.1.1.2. Multivariate analysis

PERMANOVA reflected the univariate analysis results showing significant differences in community composition between levels for both translocation and elevation factors and the interaction (Table 3a). There was a significant difference between communities without translocated *M. modiolus* clumps as a result of lower total abundance of individuals recorded in the 'control' (seafloor, no translocated *Modiolus* clumps) treatment (Table 3b). Pair-wise comparisons between elevation levels (elevated cultch, flattened cultch and seafloor) with translocated mussel clumps were not significant (Table 3b). Translocation of *M. modiolus* clumps produced faunal assemblages significantly different from all assemblages without translocated *M. modiolus* clumps (Table 3b). Multidimensional scaling (MDS) indicated separation between the 'control' (seafloor, no translocated *Modiolus* clumps) and the remainder of the artificial reef array (Fig. 4). Vectors constructed using Pearson's correlation index showed species associated with the muddy sand 'control' samples like the polychaetes *P. affinis* and *L. gracilis* and the bivalve *Thyasira flexuosa*, all typical of this substrate type, contributing the most to the separation (Fig. 4).

The effect of translocation on species composition was also indicated by the presence of distinct groupings for communities associated with both translocated *M. modiolus* and cultch treatments without translocation. Vectors indicated the main contributors to the dissimilarities for areas with translocated *M. modiolus* clumps were *M. modiolus* spat and *H. arctica.* For cultch (elevated and flattened) with no translocated *M. modiolus* clumps the main contributors were *Pomatoceros* spp. and *A. aspersa*. The MDS ordination (Fig. 4) showed no distinct separation between elevation levels either in translocated *M. modiolus* or treatments consisting only of cultch.

SIMPER analysis identified an average 47.27% similarity between the samples collected from translocated *M. modiolus* clumps with 12 taxa contributing to 50% of the similarities (Table 4a). The community was dominated by *Pododesmus* spp., *Pomatoceros* spp., *M. modiolus* spat and *L. ceratina*. Other species included infaunal and crevice dwelling species *P. longicornis*, *H. arctica*, *K. cirrata* and *Lepidonotus squamatus* and epifaunal species *A. aspersa* and *Halecium halecinum*.

Average similarity between samples collected from treatments without translocated *Modiolus* clumps was 34.65% with four taxa contributing to 50% of the similarities: *Pomatoceros* spp., *B. balanus*, *Pododesmus* spp. and *P. longicornis* (Table 4b).

The average dissimilarity between the treatments with translocated *M. modiolus* clumps was 67.35% (Table 4c). Of the total 44 taxa contributing to 50% of the dissimilarities across these samples, 15 species were epifaunal, 21 were regarded as crevice fauna and eight were infaunal. Of the 15 epifaunal taxa, *B. balanus*, *Pomatoceros* spp., *Gibbula cineraria* and *Sabellaria spinulosa* were more abundant on the scallop cultch than on translocated mussels. The remaining 11 epifaunal taxa were more abundant on the clumps of *M. modiolus*, particularly hydroids with some species uniquely associated with them including *H. halecinum*, *Sertularella polyzonias*, *Eudendrium rameum* and *Nemertesia antennina*. All of the 29 non-epifaunal taxa were more abundant in the communities associated with translocated mussel clumps. These included crevice dwelling taxa such as *H. arctica*, *Cymodoce truncata*, *Corophium sextonae*, *Harmothoe impar*, *L. squamatus* and *M. modiolus* spat. Infaunal taxa such as the polychaete *Polycirrus medusa* and the bivalves *Abra alba*, *Nucula nucleus* and *Parvicardium ovale* favoured accumulated biodeposits on the translocated clumps. Some species were unique to the clumps including the polychaetes *Aonides oxycephala*, *Ophiodrumus flexuosus* and *Polydora caeca* and the amphipods *Corophium bonelli* and *Erichtonius punctatus*.

3.1.2. Spat recruitment

Translocation was a significant factor in spat recruitment ($F_{(2, 18)} = 22.58$; $P < 0.001$) with maximum densities of 400 spat m^{-2} recorded from some of the reef plots with translocated *M. modiolus* (Fig. 5A). However, reef elevation did not significantly affect recruitment levels ($F_{(2, 18)} = 2.2$; $P = 0.119$; n.s.).

Average spat densities on translocated reef clumps (164 individuals m^{-2}) were significantly higher than on natural reefs (6 individuals m^{-2}) (Fig. 5B). ($F_{(4, 17)} = 22.15$; $P < 0.001$).

3.1.3. Survival of translocated M. modiolus

Mean frequencies of empty *M. modiolus* valves on unmodified seafloor and flattened cultch plots were similar (0.176 ± 0.16; 0.171 ± 0.15 respectively) and higher than on elevated cultch (0.064 ± 0.05) (Fig. 6). ANOVA results indicated changes in variance for translocated *M. modiolus* mortality were not significant between elevation treatments ($F_{(2, 9)}$ = 0.89; P = 0.442, n.s.).

3.2. Comparison of communities on translocated mussels on the artificial reef with natural M. modiolus *communities*

3.2.1. Univariate analysis

In total, 223 and 201 species were recorded using pooled data from reef treatments involving translocated mussel clumps and the two natural *M. modiolus* beds respectively.

There were no significant differences in species richness, diversity and evenness between the treatments consisting of translocated *M. modiolus* clumps on elevated cultch, flattened cultch and seafloor and either natural reef used in the comparison (Fig. 7 B-D; Table 5). However, total numbers of individuals (*N*) were significantly higher in the translocated clump treatments than in the two natural reefs studied (Fig. 7A; Table 5).

3.2.2. Multivariate analysis

Multivariate analysis showed a distinct separation between artificial and natural reefs (pseudo-$F_{(1, 21)}$ = 4.48; P = 0.001). The pair-wise comparisons indicated all assemblages associated with the artificial reef were significantly different from both natural reef locations (Table 6). Community composition was also significantly different between the two natural *M. modiolus* reefs sampled. The significant differences between natural and artificial reef benthic communities were reflected in the nMDS plot (Fig. 8). The plot illustrated a separation between natural and

transplanted *M. modiolus* communities but no clear groupings within the artificial reef treatments. Pearson's correlation (*r*) vectors showed that *Thyasira flexuosa* and *Owenia fusiformis* contributed the most to the separation between the communities (Fig. 8). SIMPER analysis results (Supplementary data: Appendix B) showed that the average dissimilarity between the Brown Rock and the Round Island Pinnacle natural reefs (Appendix B, Section a) was 58.79 with 31 taxa contributing to 50% of the variation.

While most taxa found in both natural reefs were also present in the translocated clump communities regardless of elevation (although in different densities), there were overall higher abundances of infaunal taxa in the former, particularly in the Round Island Pinnacle (RIP) reefs *M. modiolus* communities. Here, not only were infauna more abundant compared to the Brown Rocks (BR) beds but they were characterized by several taxa absent from the artificial reef. These included detritivourous and filter feeding taxa associated with mud or sandy mud such as *Myriochele heeri*, *Owenia fusiformis*, *Nephtys hystricis* and *Ampelisca typica* (Hayward and Ryland, 1990a, 1990b; Rainer, 1990). Overall, the communities found in the artificial reef treatments were more similar to the neighbouring BR natural *M. modiolus* communities (Fig. 1; Appendix B, Sections b, c and d) than those near RIP (Fig. 1; Appendix B, Sections e, f and g).

Average dissimilarity was lowest between the communities on elevated cultch and at the Brown Rocks site (72.32%). In total, 22 taxa were more abundant in the artificial reef, mainly encrusting species (e.g. *B. balanus*, *Pododesmus* spp. and *Pomatoceros lamarcki*) but also crevice fauna (e.g. *H. arctica*, *Liljeborgia pallida* and *Corophium sextonae*) and epifauna (e.g. *Sertularia* sp. and *H. halecinum*). Ten species found in the BR *M. modiolus* community were absent from the artificial reef community, mainly infaunal species associated with muddy sand substrata (e.g. *O. fusiformis*, *Notomastus latericeus* and *Caulleriella* sp.) but also the crinoid *Antedon bifida*, frequently recorded on natural *M. modiolus* beds (Appendix B, Section b). The average dissimilarity between the communities on flattened cultch and at Brown Rocks was 73.19%. Forty-four taxa contributed to 50% of the dissimilarity, 34 of which were more abundant in the artificial reef treatments (Appendix B, section c). Only 10 of all species found at Brown Rocks were absent from the flattened cultch treatment, including *A. bifida*. Finally, community composition in *M. modiolus*

translocated onto seafloor showed 74.25% dissimilarity from the natural Brown Rocks community. Most of the 48 taxa responsible for 50% of the dissimilarity between natural and artificial reefs were more abundant in the communities associated with the translocated treatments (Appendix B, Section d). Species which were more abundant in the natural reefs than in mussel clumps translocated onto seafloor included both infauna (*N. nucleus*, *Caulleriella* sp, *M. palmata* and *N. latericeus*) and epifauna (*A. bifida* and *A. aspersa*).

The elevated cultch and the RIP community were 80.06% dissimilar and 44 taxa contributed to 50% of the variation in community composition (Appendix B, Section e). The flattened cultch and RIP communities were 79.22% dissimilar with 40 taxa contributing to 50% of the variation (Appendix B, Section f). The *M. modiolus* on seafloor treatment was less dissimilar to the RIP beds with an average dissimilarity of 77.84%. In total, 43 taxa contributed to 50% of the dissimilarity (Appendix B, Section g). The vast majority of the species contributing to the dissimilarities were more abundant in the translocated mussel treatments. These species included epifauna (e.g. *B. balanus*, *Pododesmus* sp. and *Scypha ciliata*), crevice fauna (e.g. *M. modiolus* spat, *H. arctica*, *L. ceratina* and *S. inflatum*) and some species not recorded from the natural reef (e.g. *C. truncata*, *H. arctica*, *H. halecinum*, *S. ciliata* and several species of small gastropods). In contrast, most species recorded in higher abundances in the natural reef were predominantly infaunal (e.g. *Glycera tridactyla*, *Lumbrineris latreilli*, *O. fusiformis*, *T. stroemi*, *Melinna palmata*, *T. flexuosa* and *Timoclea ovata*). Some crevice fauna (e.g. *Scalibregma inflatum*, *Pholoe synophthalmica* and *Nephtys histrycis*) and epifaunal taxa (e.g. *A. aspersa* and *Callochiton achatinus*) were also more abundant in the natural reef.

Dominance curves calculated for the natural reefs and translocated *M. modiolus* treatments showed relatively low cumulative dominances in all assemblages. The dominance curves for *M. modiolus* on uncultched substrate and the natural reefs had the lowest intersects with the ordinate axis (< 20%) suggesting their faunal assemblages are slightly more heterogeneous than those associated with *M. modiolus* on elevated and flattened cultch (Fig. 9).

4. Discussion

Successful restoration of a species involves a combination of restocking and redressing the loss of its habitat (Caddy and Defeo, 2003; Brumbaugh et al., 2006; Brumbaugh and Coen, 2009) as well as removing the cause of its decline. In shellfish restoration programs this approach is logistically complex and costly involving the translocation of key reef-forming species onto three-dimensional reefs constructed from large quantities of cultch. Therefore it is essential to test the contribution of each element of the restoration to its overall success.
After one year, translocated *M. modiolus* clumps had significantly richer and more diverse faunal assemblages with higher densities of recruited spat than control areas outside the artificial reef and treatments consisting solely of shell cultch.

4.1. Community composition and M. modiolus *spat recruitment on different reef types 12 months after construction*

4.1.1. Community composition

Translocation of *M. modiolus* had a significant effect on the diversity and composition of the associated faunal assemblage. In total, 223 taxa were recorded in the artificial reef array, 193 of which were found in translocated mussel treatments and 105 in treatments without translocated mussel clumps. In seafloor ‘control’ areas (no cultch, no translocation) only 64 taxa were recorded. Species richness, diversity and evenness were significantly higher in all artificial-reef treatments that included translocated *M. modiolus* clumps than in those comprising bare scallop shell. However, although higher numbers of species and total abundance of individuals were recorded from translocated mussel clumps than from nearby seafloor controls, evenness (*J*) and diversity (*H’*) indexes were not significantly different between them. This suggests that both the artificial reef and the damaged *Modiolus* reefs used as controls might be at comparable successional stages with a similar, but not identical, mixture of taxa.

Similarities between treatments may be explained by the presence of small scavengers, predators and other crevice-dwelling species in interstices between the scallop shells and the transplanted mussels. Species recorded on both translocated *M. modiolus* and natural reefs communities included *Harmothoe* spp., *L. squamatus*, *K. cirrata*, *P. longicornis, M. modiolus* spat, *Sphenia binghami* and *H. arctica*. All species are commonly associated with *M. modiolus* communities (George and Warwick, 1985; Jones, 1951; Mair et al., 2000; Ojeda and Dearborn, 1989; Rees et al., 2008; Roberts et al., 2011; Rowell, 1967). Communities recorded in both translocated *M. modiolus* (regardless of cultch) and natural assemblages matched the species composition of a *Modiolus* community *sensu* Thorson (1957). Significant differences between treatments with and without translocated mussel clumps can be linked to the structural complexity of the habitat created by the mussels, which is similar to natural *M. modiolus* beds (Ojeda and Dearborn, 1989; Sanderson et al., 2008) as a result of mussel clumping behaviour. The attraction of epifauna towards horse mussel clumps could be the result of their three-dimensional configuration influencing small-scale local hydrodynamic patterns. As individual mussels orient themselves in different directions, turbulence increases POM suspension providing ideal feeding conditions for sessile epifauna. This phenomenon has been reported in *M. edulis* beds (Butman et al., 1994; Frechette, 1989) and is likely to occur on *M. modiolus* reefs as suggested by Ojeda and Dearborn (1989). An additional, related, effect of *M. modiolus* translocation, which affects community composition, is biodeposition of particulates. Although not quantified, there was much higher retention of sediment and pseudofaeces amongst the mussel clumps than on cultch (elevated and flattened) without translocated mussel clumps (personal observations). These biodeposits became occupied by infaunal taxa such as *A. alba*, *N. nucleus*, *Mya* spp. and *M. bidentata* which are usually found in sand and muddy sand (Hayward and Ryland, 1990a). Rees et al. (2008) also reported *A. alba* and *M. bidentata* as common in the mud accumulated amongst *M. modiolus* clumps and on empty valves.

Infaunal species were either less abundant or completely absent from bare cultch treatments. However, several species recorded in the translocated mussel community were also found amongst the elevated and flattened cultch without translocated mussel clumps, albeit in much lower abundances (Table 4c). Species

such as *H. arctica*, *L. ceratina*, *A. alba*, *L. squamatus*, *P. ovale* and more importantly, *M. modiolus* spat, were all found in the latter treatments but were likely to experience increased predation in the more exposed scallop valves.

The significant increase in community richness and diversity observed in areas where mussel translocation occurred is probably a result of the combined effects of predation refuge and increased habitat availability as a result of structural complexity and increased sedimentation (Navarro and Thompson, 1997; Witman, 1985). Thus, the presence and clumping behaviour of *M. modiolus* appear to have been the key element in rapidly establishing a diverse community on the artificial reef similar to natural horse-mussel communities (Holt et al., 1998; Magorrian and Service, 1998; Hiscock et al., 2004).

4.1.2. Spat recruitment

The densities of *M. modiolus* spat recorded on the elevated cultch treatments were not significantly higher than on the flattened and seafloor treatments. Therefore, the initial hypothesis of elevation being beneficial for recruitment was rejected. However, spat recruitment was significantly enhanced by translocation of clumped *M. modiolus* (Fig. 5A). Experimental work carried out prior to the present study found no *M. modiolus* recruitment on cultch deployed on trays after more than one year on the seabed. By contrast, small numbers of *M. modiolus* spat settled amongst clumps of live *M. modiolus* deployed on trays over the same period (personal observation; Roberts et al., 2011). It is likely that *M. modiolus* preferably settles amongst conspecifics as high spat fall densities have been reported in the clumps of live *M. modiolus* by other authors (Roberts, 1975; Rees et al., 2008). In addition, the complex network of micro-crevices created by the matrix of byssus threads and shell fragment found within the clumps of live *M. modiolus* provides an environment where spat can escape predation. Contrary to Schulte et al. (2009), Nestlerode et al. (2007) found elevation in subtidal oyster reefs was not a significant factor for settlement and survival of oyster spat. Significantly higher recruitment in oyster cultch compared to clam cultch, was attributed to both preferential oyster settlement behaviour and higher survival rates in the more structurally complex oyster cultch. Similarly, the recruitment patterns observed in the artificial *M. modiolus* reef array may also be

explained as a combination of preferential settlement and lower predation rates coupled with increased feeding opportunities as a result of biodeposition and increased turbulence around the clumps.

Total spat numbers for the area occupied by translocated clumps were an order of magnitude higher than the two natural *M. modiolus* reefs studied in Strangford Lough used in the comparison (Fig. 5B). It could be argued the differences observed reflect seasonality in *M. modiolus* recruitment in Strangford Lough as sampling in the artificial reef took place in March 2011 whereas natural reefs were sampled in December 2010. However, Brown and Seed (1976) suggested that in Strangford Lough *M. modiolus* recruitment is continuous. The higher spat fall rates are likely the result of higher substrate availability offered by *M. modiolus* translocated in densities of up to 200 clumped mussels m^{-2}. Such high concentrations of mussels provided a much bigger area of suitable settlement substrate than any extant natural 'pristine' bed in Strangford Lough, i.e. Round Island Pinnacle (RIP) and Craigyouran (Fig. 1). These *M. modiolus* beds at their best consist of five to 15 mussels per clump, with maximum densities of 50 mussels m^{-2} (Roberts et al., 2011).

A recent particle dispersal study by Elsäßer et al.(in review) indicated high near-source particle retention which suggests the remnant *M. modiolus* subpopulations in Strangford Lough are largely self-recruiting. The artificial reef is, therefore, mostly isolated from the larval sources in the east section of the Lough (including RIP) but it experiences strong connectivity with the Brown Rocks (BR) natural beds 1 km to the north. According to Elsäßer et al. model, hydrodynamic and larval supply conditions in the artificial reef are similar to those in the nearby natural BR beds which further suggests that recruitment limitations in natural beds are probably the result of density related, Allee effects (Allee, 1931).

In addition, *M. modiolus* settlement could be enhanced by the dense tunicate which covered cultch and seafloor treatments six months after construction as it facilitates hydroid colonization in the early stages of the succession. Pediveligers of *M. modiolus* may, like those of *Mytilus edulis* (Seed, 1969), settle primarily on hydroids and later migrate to crevices and other refuges.

4.1.3. Survival of translocated mussels

Average mortalities of translocated mussels were very low but not significantly different between all treatments after the 12-month period. Appropriate site selection and reef construction methodologies probably minimised the effect of physical stress and predation. However, it was hypothesised reef elevation would increase the survivorship of translocated *M. modiolus* as found in restored *Crassotrea virginica* reefs in the USA (Lenihan, 1999; Schulte et al., 2009). The majority of the existing examples and shellfish restoration guidelines are designed with oyster species in mind. Many of the areas where these restoration programmes have been undertaken are low energy, estuarine systems and in some cases already suffering from pollution, eutrophication and hypoxia (Lenihan and Peterson, 1998; Powers et al., 2005; Johnson et al., 2009). Therefore low relief oyster reefs are prone to experience lack of nutrients, hypoxic conditions, higher siltation and increased disease as a result of reduced water flow. These effects can potentially reduce survival and the effectiveness of a shellfish reef restoration program (Brumbaugh et al., 2006; Jordan-Cooley et al., 2011; Lenihan and Peterson, 1998) but may be overcome by reef elevation (Schulte et al., 2009). Reef elevation might not be critical for the survival of *M. modiolus* because of its infaunal (Comely, 1978) and semi-infaunal (Meadows and Shand, 1989) life habits but may become more critical over time.

4.2. Comparisons of communities on translocated mussels on the artificial reef with natural M. modiolus *communities.*

One of the metrics to assess artificial reef performance should be 'the return of naturally, diverse assemblages of species to the restored habitat or ecosystem' (Brumbaugh et al., 2007) and the convergence towards the 'natural' community to be restored (Jensen, 2002; Walters and Coen, 2006). Faunal assemblage differences between the reef array and the seafloor without translocated mussels were significant for all metrics used. Therefore translocation of *M. modiolus* clumps

created a rich community in an otherwise species–poor, damaged *M. modiolus* biotope.

To evaluate whether the assemblage found in the community associated with translocated *M. modiolus* clumps converged towards a natural *M. modiolus* community, natural reefs used in the comparison should be adjacent to the artificial reef and in relatively undisturbed condition (Carr and Hixon, 1997). The natural reefs chosen for the comparison study were the best examples of a relatively undisturbed *M. modiolus* community in Strangford Lough but are not pristine (Roberts et al., 2011).

The results of the univariate analysis comparisons indicated all three translocation reef treatments performed well as they showed no significant differences in all indexes with the exception of higher abundance of specimens (*N)* associated with the translocated mussel community.
Multivariate analysis indicated a divide between the faunal assemblages associated with natural *M. modiolus* beds and translocated clumps 12 months after the construction of the experimental reef array. The dissimilarities between the transplanted *M. modiolus* communities and natural reefs were overall high although the Round Island Pinnacle (RIP) reef was slightly less similar. The RIP *M. modiolus* beds consist of more frequent clumps with more mussels per clump than Brown Rocks (BR) according to Roberts et al. (2011) and therefore are likely to harbour a higher number of species than the more fragmented beds at BR, particularly those species associated with the interstitial matrix. In spite of these differences, SIMPER analysis clearly showed that both assemblages were characterised by a very similar array of species differing only in their relative abundances. The observed correlation between the presence of dense *M. modiolus* clumps and higher faunal abundance has been previously suggested to explain the differences in community composition between ridges and troughs in horse mussel bioherms in the Irish Sea (Rees, 2009; Sanderson et al., 2008) while Ojeda and Dearborn (1989) also indicated that increased biodiversity was also dependent on the size of the horse mussel clumps. The observed differences in total abundances between the natural and artificial *M. modiolus* reef communities were a likely consequence of the much wider area available for settlement offered by the combined presence of *M. modiolus* clumps and scallop shell cultch in the artificial reef array, particularly when compared to the

patchy clump distribution that characterise the remaining natural *M. modiolus* beds in Strangford Lough. Most taxa contributing to the dissimilarities were encrusting and crevice fauna found in higher abundances in the transplanted *M. modiolus* where the availability of microhabitats was higher than in other treatments. However, one of the effects of increased reef elevation is faster current flow in the reef crest compared with the reef base or low profile reefs which reduces siltation and biodeposition (Lenihan, 1999). The effect of elevation, although beneficial for the survival and recruitment of the keystone species (Schulte et al., 2009) likely contributed to the lower richness and abundance of infaunal taxa in the translocation treatments compared to natural *M. modiolus* beds which in Strangford Lough have much lower elevation.

M. modiolus communities at Round Island Pinnacle and Brown Rocks are currently very fragmented consisting of sparse, non-continuous clumps of 5 to 10 mussels (Roberts et al., 2011). Translocated mussels in the artificial reef on the other hand consist of dense patches of ca. 200 mussels m^{-2}. Comparison of artificial reef treatments with and without transplanted *M. modiolus* with natural reefs, revealed lower species abundances of epifaunal and crevice invertebrate taxa in natural *M. modiolus* beds which could also be the result of higher predation pressure. Relaid mussels in all treatments including seafloor clumped quickly and remained epifaunal 12 months after reef construction whereas *M. modiolus* in natural beds are mainly infaunal or semi-infaunal. The increased predation in natural beds is probably a combination of reduced access to the shelter provided by the matrix of byssus threads as suggested by Holt et al. (1998) and the loss of the elevation observed in damaged biogenic reefs which facilitates access to predators (Soniat et al., 2004). The community recorded in the translocated *M. modiolus* clumps, regardless of reef elevation, was comparable in number of taxa to most natural semi-infaunal *M. modiolus* communities in the North Atlantic, both in Europe and in North-America. Only reefs off Nova-Scotia were richer, the results probably influenced by the wider sampling area and the sampling gear used (Table 7). Data available from *M. modiolus* communities in the USA and Canada only included epifaunal species which explains the low numbers of taxa when compared to the artificial reef. Species diversity (*H'*) and evenness (*J*) data were only available from Scottish (Mair et al., 2000) and Welsh (Rees et al., 2008) *M. modiolus* beds. Evenness values were very similar compared to the artificial reef; however, species diversity (*H'*) in the

experimental reef was low compared to the mature, relatively undisturbed Welsh *M. modiolus* bioherms and Scottish semi-infaunal beds.

It is still too early to determine how communities associated with translocated horse mussels will develop over time as *M. modiolus* is long lived reaching ages well over 40 years (Anwar et al., 1990). The longevity and slow growth of *M. modiolus* suggests climax communities associated with established beds also develop over a long period of time (Holt et al., 1998; Rees, 2009). The similar evenness index values and dominance curves in both natural and translocated *M. modiolus* communities are interpreted not as an indication of the development of a climax *Modiolus* community associated with the translocated mussels after only 12 months, but rather as a confirmation that *Modiolus* communities in Strangford Lough are still recovering from the disruption they experienced 20 years ago

5. Conclusions

Few artificial reefs have been deployed for ecological restoration in Europe outside the Mediterranean where they have been used as barriers to protect seagrass *Posidonia* meadows (Allemand et al., 2000; González-Correa et al., 2005; Sánchez-Jerez et al., 2002) and coralligenous bedrock (Charbonnel and Bachet, 2011). In the United Kingdom artificial reefs have been solely deployed to investigate biotic colonization and attraction of commercial species using inert materials such as quarried rock or concrete blocks (Jensen, 2002; Burt et al., 2011). However, only 50% of artificial reefs achieve all their objectives (Baine, 2001). The artificial reef in Strangford Lough is globally unique in its objective to restore habitat formed by the horse mussel *M. modiolus*.

The results of a one year monitoring survey should be considered with caution as communities develop over a long period of time and very little is known regarding succession in *M. modiolus* communities. Studies on community development in artificial reefs show that although composition is more similar with increasing age, convergence is rarely achieved (Burt et al., 2011). In some cases it has been suggested that at least 10 years are necessary to observe convergence between natural and artificial reefs (Perkol-Finkel and Benayahu, 2005).

Nevertheless, using Baine's model, which ranks reef performance on a scale from -3 (total failure) to +3 (total success) (see Table 5 in Baine, 2001) the Strangford Lough Artificial *Modiolus* reef achieves a score of +2 based on the following criteria:

1. *Reef objectives*. The main objective was to determine whether translocation of adult live mussels onto an artificial reef was an effective strategy to stimulate recovery. This was achieved as the artificial reef: (a) Stimulated re-colonization by a faunal assemblage similar in species composition and richness to natural *M. modiolus* communities; and (b) significantly enhanced the recruitment of juvenile horse mussels to the population. However, because convergence with the two natural *M. modiolus* reefs used in the multivariate analysis was not achieved this objective was achieved only in part.

2. *Benefits to the local environment or sea users are realised by the reef's creation*. *M. modiolus* clump translocation successfully increased biodiversity and recruitment of juvenile *M. modiolus* on otherwise species-poor, muddy substrata. Some of the species attracted to the artificial reef included juvenile fish, crustaceans and bivalves suggesting it could be used as a nursery area for some species of commercial interest. The increase in juvenile horse mussels recruited to the population could also contribute to improved water quality in Strangford Lough.

3. *Minor changes to design or management may be warranted but are not critical.* Overall the reef design was successful as all treatments studied achieved the original objectives. After 12 months it was concluded that addition of cultch, whether it was elevated or flattened, did not increase faunal diversity, recruitment of juvenile *M. modiolus* or translocated mussel survival to significant levels compared to the treatments consisting only of transplanted mussels onto the seafloor. As suggested by Nestlerode et al. (2007) for *Crassostrea virginica*, settlement substrate preference and not reef elevation was the main factor limiting the success of the experimental reef array. Elevation over 0.5 m as used in this study is likely to be excessive as natural beds in Strangford Lough are normally only raised 0.1 to 0.5 m above the bottom in pristine conditions (personal observations). Elevation did not provide significant advantages and in some respects might have been detrimental for the development of the typical *M. modiolus* communities, as stronger flow might have reduced siltation and resulted in a lower number of infaunal species compared to natural reefs. Therefore it is recommended that future restoration efforts consist only

of translocation of adult *M. modiolus* thus avoiding the extra cost and effort of sourcing and deploying cultch.

4. *Research reefs that have provided useful data for the assessment of localised reef performance and management.* The experimental *M. modiolus* reef array is the first of its kind and has provided new data on the development of the faunal community associated with translocated *M. modiolus* used for restoration of natural biogenic reefs. The data collected will be incorporated into future monitoring programs.

The *M. modiolus* communities remaining in Strangford Lough are not recovering naturally and could disappear in the near future (Roberts et al., 2011). As found with impacted coral reefs (Rinkevich, 2005), the remaining *M. modiolus* communities in Strangford Lough are unlikely to recover naturally from anthropogenic stress without intervention. Using metrics developed by Baine (2001) to assess reef performance confirmed translocation of *M. modiolus* clumps onto an artificial reef was a successful restoration technique as it enhanced natural recruitment of *M. modiolus* spat and increased biodiversity in a damaged *M. modiolus* habitat.

This is a straightforward intervention strategy that is amenable to experimental manipulation and likely to be successful in the future restoration of impacted biogenic reefs.

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Figure captions

Fig. 1. Map of Strangford Lough, Northern Ireland (U.K.) showing the position of the artificial reef array and the locations of natural *M. modiolus* reefs where benthic sampling was undertaken. Rectangles represent 'No fishing zones' implemented in March 2011 by the Northern Irish Executive.

Fig. 2. (A) Position of the experimental *M. modiolus* reef constructed in Strangford Lough, Northern Ireland. (B) Schematic representation of the artificial reef array and control plots. All positions and relative dimensions are indicative and not to scale.

Fig. 3. Box plots of (A) total number of individuals (*N*); (B) Margalef's species richness (*d*); (C) Shannon-Wiener's species diversity (*H'*); and (D) Pielou's evenness (*J*) grouped by reef elevation and *M. modiolus* translocation treatments 12 months after reef construction. The box represents the inter-quartile range, with a line indicating the median and whiskers extending to the maximum and minimum observed values. Grey and white boxes indicate translocation treatments with and without *M. modiolus* respectively.

Fig. 4. nMDS ordination based on Bray-Curtis similarity matrix of fourth root transformed quadrat removal data taken on the artificial reef array 12 months after construction. Treatments: Black filled shapes indicate presence of translocated *Modiolus* clumps. Grey-filled shapes indicate no translocation. Squares = Elevated cultch; semi-circles = flattened cultch, flat lines = seafloor. Grey circles represent 40% group similarity. Vectors are based on Pearson's correlation indexes (r) and were calculated for the species contributing the most to the dissimilarities between treatments observed in the SIMPER analysis (Table 4). Stress level (0.15) indicates useful two-dimensional data representation.

Fig. 5. *M. modiolus* spat recruitment: (A) comparison between artificial reef treatments with (grey boxes) and without translocated horse mussels (white boxes) (n = 12); (B) comparison between artificial reef treatments with translocated *M. modiolus* (n = 12) (grey boxes) and natural *M. modiolus* beds sampled in Strangford Lough (n = 10) (white boxes). The box represents the inter-quartile range, with a line indicating the median and whiskers extending to the maximum and minimum observed values.

Fig. 6. Boxplots comparing mortality frequencies of *M. modiolus* between different elevation treatments 12 months after completion of the artificial *M. modiolus* reef array. Mortality was calculated as the ratio between the empty *M. modiolus* valves divided by 2 and the total number of *M. modiolus* counted in each 0.25 m^2 quadrat. The box represents the inter-quartile range, with a line indicating the median and whiskers extending to the maximum and minimum observed values.

Fig. 7. Box plots of (A) total number of individuals (*N*), (B) Margalef's species richness (*d*), (C) Shannon-Weiner diversity (*H'*) and (*D*) Pielou's evenness (*J*) in artificial (grey boxes) and natural *M. modiolus* reefs (white boxes). The box represents the inter-quartile range with a line indicating the median and whiskers extending to the maximum and minimum observed values. Ordinate axis legend: Artificial reef treatments with translocated *M. modiolus*: Ec = Elevated cultch; Fc = Flattened cultch; Sf = Sea floor; Natural *M. modiolus* reefs surveyed in Strangford Lough: BR=Brown Rocks; RIP=Round Island Pinnacle (Fig.1).

Fig. 8. nMDS ordination based on Bray-Curtis similarity matrix of log (x+1) transformed quadrat removal data showing distinct separation between faunal assemblages associated with extant natural *M. modiolus* beds in Strangford Lough, Northern Ireland and communities associated with *M. modiolus* translocated onto elevated and flattened cultch and on seafloor 12 months after reef construction. Natural beds are represented in grey: crosses = Brown Rocks; triangles = Round Island Pinnacle). Experimental reef array with translocated *M. modiolus* is represented by solid black figures: semi-circles = elevated cultch; squares = flattened cultch; lines = seafloor. The taxa contributing the most to the dissimilarity between the artificial and natural *M. modiolus* reefs (Appendix B, Supplementary data) are displayed as Pearson's correlation vectors. The stress level (0.09) shows good representation of the data.

Fig. 9. *K*-dominance curves for faunal communities comparing artificial reef (AR) treatments (open triangles) and natural *M. modiolus* beds sampled from Round Island Pinnacle (RIP) and Brown Rocks (BR) (solid figures).

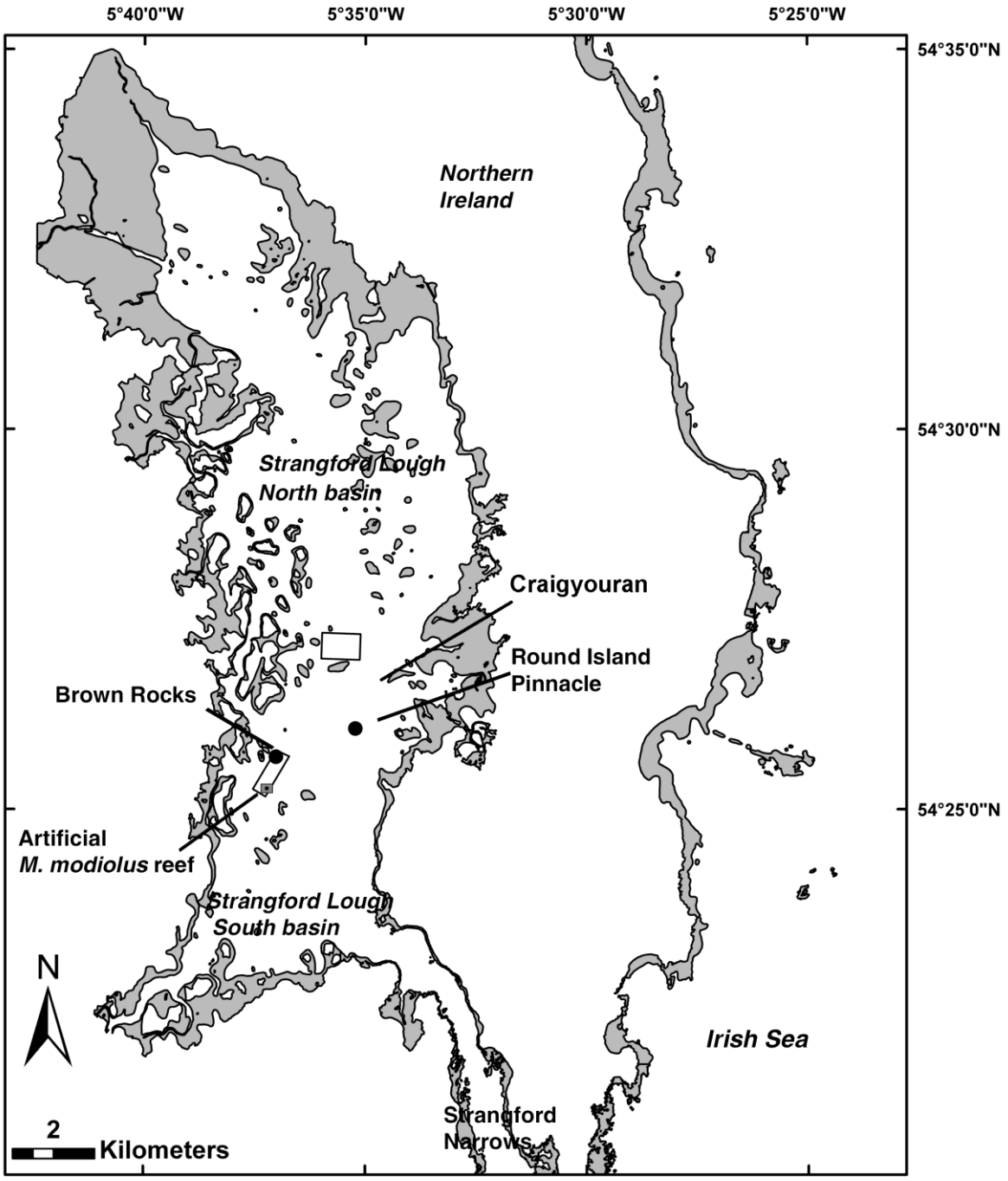

Fig. 1

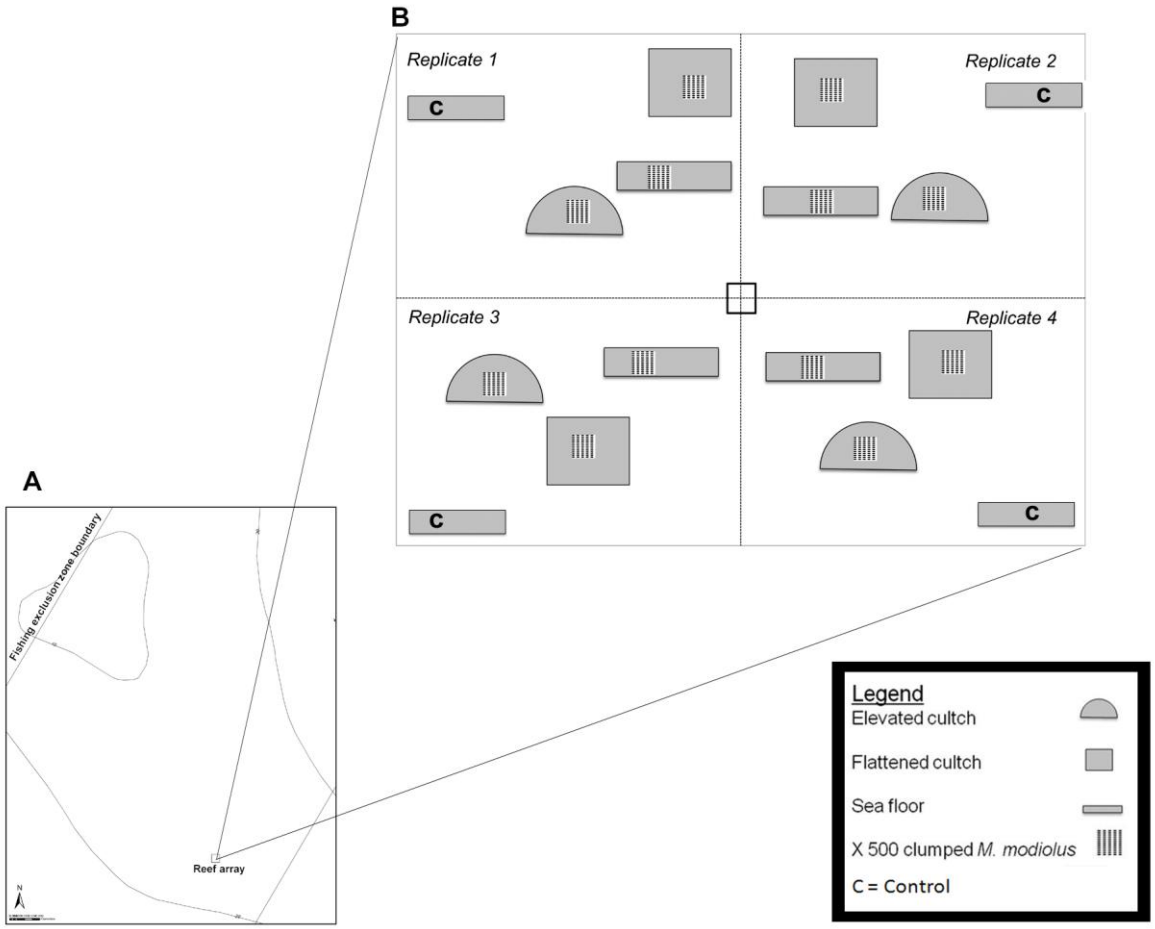

Fig. 2

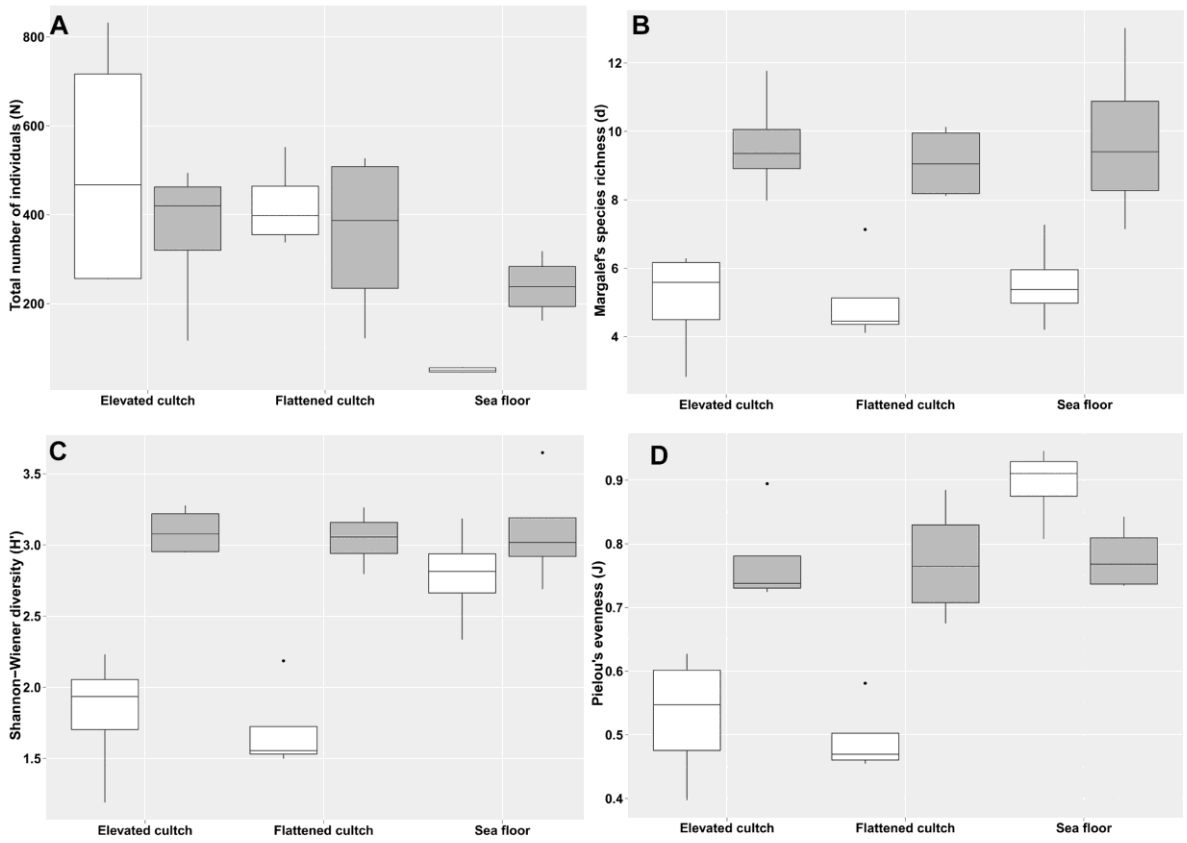

Fig. 3

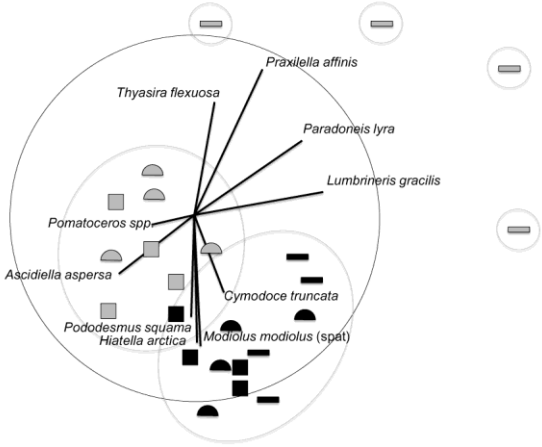

Fig. 4

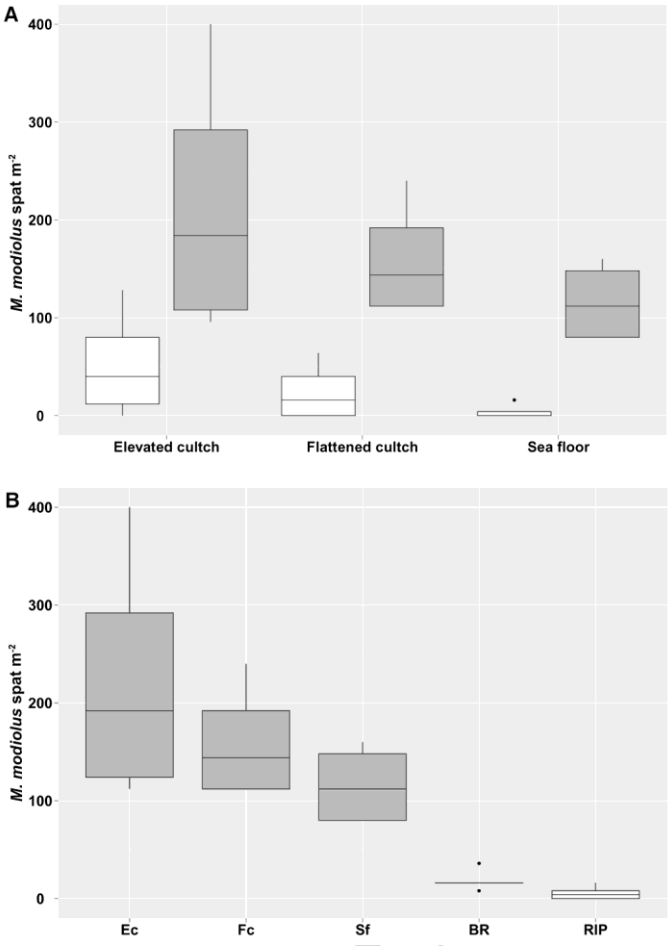

Fig. 5

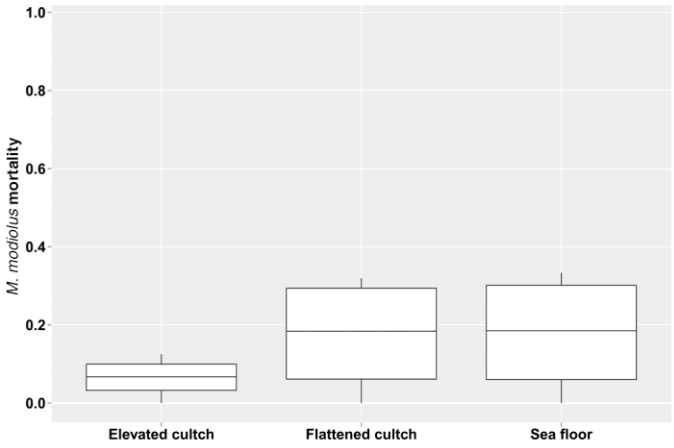

Fig. 6

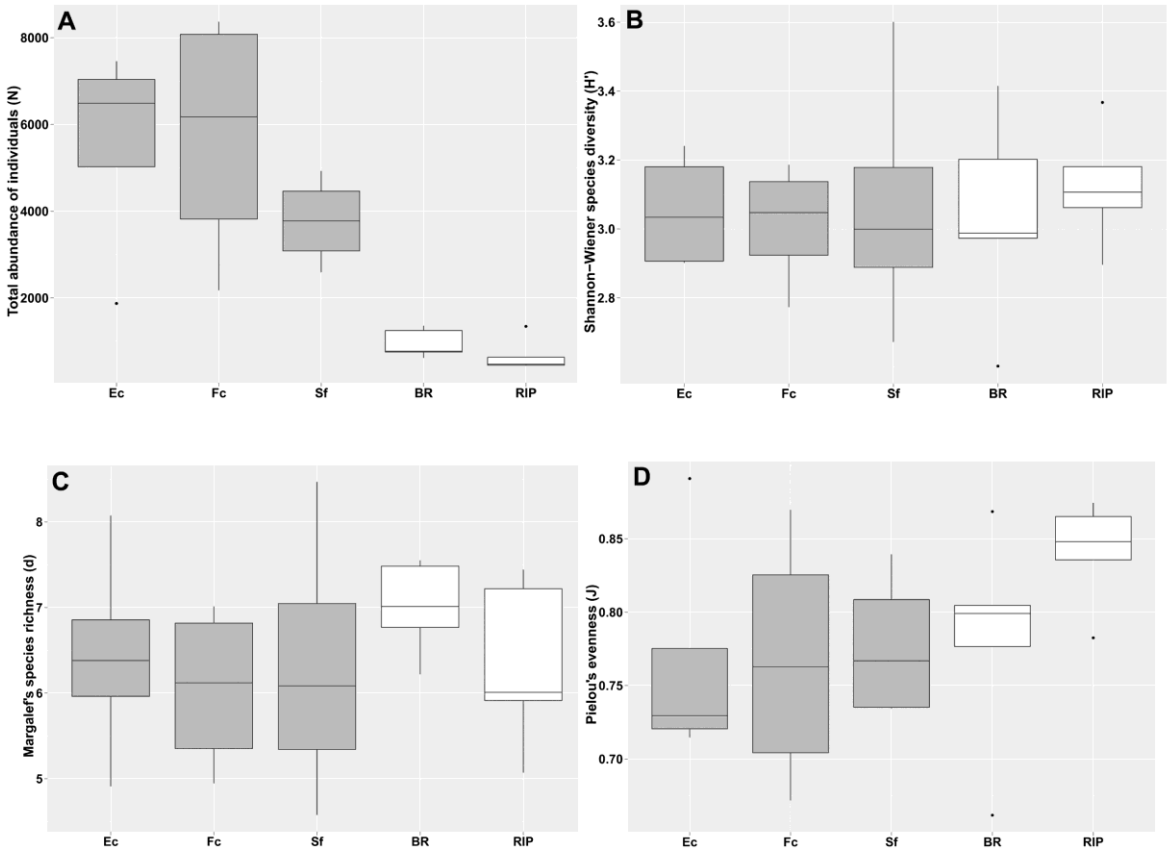

Fig. 7

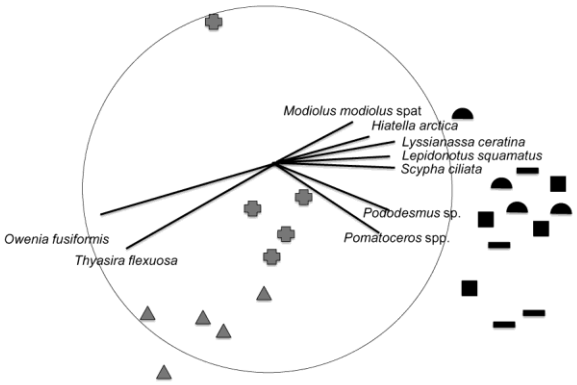

Fig. 8

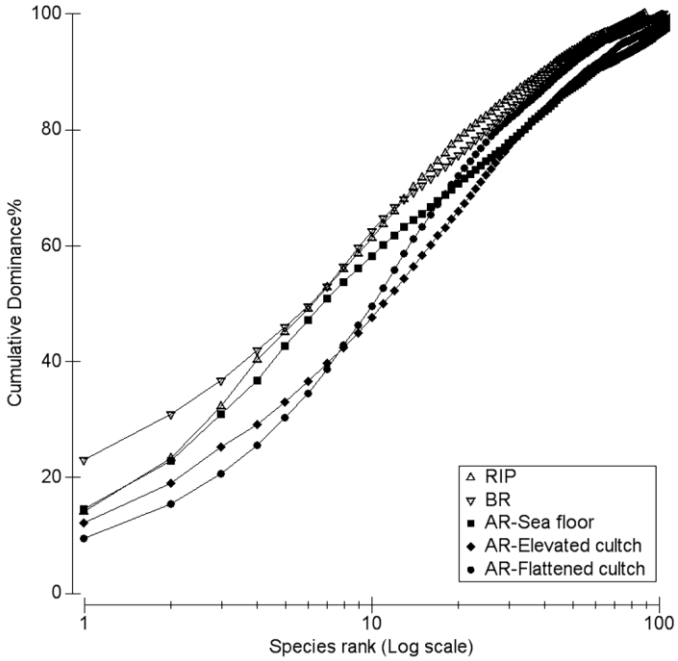

Fig. 9

Table 1

Top 100 most abundant taxa[a] recorded from quadrat removal samples taken at the *M. modiolus* artificial reef[b] 12 months after construction.

Taxon	%	Taxon	%	Taxon	%
Pomatoceros spp.	23.00	*Eudendrium rameum*	0.28	*Psammechinus milliaris*	0.12
Balanus balanus	19.56	*Stylostomun ellipse*	0.28	*Nemertesia antennina*	0.10
Pododesmus spp.	7.17	*Pomatoceros triqueter*	0.28	*Ampelisca tenuicornis*	0.10
Pisidia longicornis	3.27	*Asterias rubens*	0.27	*Maera othonis*	0.10
Lyssanasa ceratina	2.94	*Hydroides norvegica*	0.23	*Gnathia maxillaris*	0.10
Modiolus modiolus (spat)	1.85	*Apseudes talpa*	0.21	*Brachystomia rissoides*	0.10
Hiatella arctica	1.70	*Parvicardium ovale*	0.21	*Palliolum striatum*	0.10
Kefersteinia cirrata	1.49	*Sabellaria spinulosa*	0.19	*Cerebratulus fuscus*	0.09
Cymodoce truncata	1.33	Ostracoda sp.	0.19	*Eulalia viridis*	0.09
Abra alba	1.16	*Eudendrium rameum*	0.18	*Syllidia armata*	0.09
Ascidiella aspersa	1.16	*Sertularella gayi*	0.18	*Paradoneis lyra*	0.09
Terebellides stroemi	1.06	*Alcyonidium diaphanum*	0.18	*Scalibregma inflatum*	0.09
Spirorbidae indet.	0.89	*Tubulanus annulatus*	0.17	*Owenia fusiformis*	0.09
Sertularella polyzonias	0.87	*Abietinaria abietina*	0.15	*Trichobranchus glacialis*	0.09
Gibbula cineraria	0.81	*Platynereis dumerilii*	0.14	*Parvicardium scabrum*	0.09
Sertularia spp.	0.77	*Lumbrineris gracillis*	0.14	*Ophiodromus flexuosus*	0.08
Polycirrus medusa	0.75	*Aonides oxycephala*	0.14	*Mytilus edulis*	0.08
Harmothoe impar	0.71	*Halopteris catharina*	0.13	*Obelia dichotoma*	0.06
Liljeborgia pallida	0.71	Turbellaria indet..	0.13	*Alcyonum digitatum*	0.06
Ophiothrix fragilis	0.70	*Cirratulus cirratus*	0.13	*Lineus longissimus*	0.06
Lepidonotus squamatus	0.63	*Praxilella affinis*	0.13	*Glycera tridactyla*	0.06
Scypha ciliata	0.54	*Thoralus cranchii*	0.13	Mysidacea sp.	0.06
Halecium halecinum	0.52	*Emarginula rosea*	0.13	*Anthura gracilis*	0.06
Orchomene nana	0.46	*Capulus ungaricus*	0.13	*Thyasira flexuosa*	0.06
Corophium sextonae	0.46	*Chlamys varia*	0.13	*Flustra foliacea*	0.06
Corophium bonnelli	0.45	*Palliolum tigerinum*	0.13	*Amphipholis squamata*	0.06
Nucula nucleus	0.44	*Bugula flabelata*	0.13	*Myrianida pinnigera*	0.05
Eumida sanguinea	0.41	*Leucosolenia botrilloides*	0.12	*Aonides paucibranchiata*	0.05
Musculus costulatus	0.36	*Halichondria panicea*	0.12	*Branchiomma bombyx*	0.05
Pholoe inornata	0.35	*Plumularia setacea*	0.12	*Paradoneis lyra*	0.09
Flabelligera affinis	0.35	*Harmothoe* sp.	0.12	*Scalibregma inflatum*	0.09
Brachystomia scalaris	0.32	*Capitella capitata*	0.12	*Owenia fusiformis*	0.09
Sphenia binghami	0.32	*Achelia echinata*	0.12		
Pherusa plumosa	0.31	*Leptochiton asellus*	0.12		

[a] Relative abundances are indicated as the percentage of the total faunal abundance.

[b] Results were pooled from all reef elevation and translocation treatments.

Table 2

Summary of two-way ANOVA results testing the differences in the total abundance (*N*), species diversity (*H'*), species richness (*d*) and evenness (*J*) between the faunal communities associated with elevation (elevated cultch, flattened cultch and seafloor) and *M. modiolus* translocation (present, absent). Quadrat removal sampling data obtained 12 months after artificial reef construction.

Variable	**Source of variation**	**d.f.**	***F*-ratio**	***P***
Total abundance (*N*)	Translocation	1	0.01	0.921
	Elevation	2	6.93	**<0.01**
	Interaction	2	2.15	0.145
Shannon-Wiener species diversity (*H'*)	Translocation	1	51.96	**<0.001**
	Elevation	2	6.86	**<0.01**
	Interaction	2	6.13	**<0.01**
Margalef's species richness (*d*)	Translocation	1	40.61	**<0.001**
	Elevation	2	0.26	0.775
	Interaction	2	0.05	0.953
Pielou's evenness (*J*)	Translocation	1	18.51	**<0.001**
	Elevation	2	16.84	**<0.001**
	Interaction	2	15.95	**<0.001**

d.f. = degrees of freedom. Bold font indicates significant differences at the 0.05 cut-off point.

Table 3

Multivariate analysis of variance (PERMANOVA) (a) and pair-wise *post hoc* analysis results (b) showing significant differences in the faunal assemblages associated with the translocation and elevation treatments 12 months after construction of the experimental reef array.

a)

Source	*d.f.*	*SS*	*MS*	*Pseudo-F*	*P*
Translocation	1	7732	7732	4.97	**0.001**
Elevation	2	7011.5	3505.8	2.25	**0.001**
Interaction	2	4965.4	2495.6	1.59	**0.012**
Residuals	18	28008	2482.9		

b)

Groups	*t*	*P*
Within level 'Absent' of factor 'M. modiolus *translocation'*		
Sea floor, Elevated cultch	1.77	**0.045**
Sea floor, Flattened cultch	1.72	**0.026**
Elevated cultch, Flattened cultch	0.98	0.599
Within level 'Present' of factor 'M. modiolus *translocation'*		
Sea floor, Elevated cultch	1.13	0.19
Sea floor, Flattened cultch	1.16	0.167
Elevated cultch, Flattened cultch	0.95	0.664
Within level 'Sea floor ' of factor 'Elevation'		
M. modiolus present, absent	1.67	**0.031**
Within level 'Elevated cultch' of factor 'Elevation'		
M. modiolus present, absent	1.46	**0.024**
Within level 'Flattened cultch' of factor 'Elevation'		
M. modiolus present, absent	1.79	**0.03**

Significant *P* values (α = 0.05) indicated by bold font style. (d.f. =Degrees freedom; SS = Sums of squares; MS = Mean square).

Table 4

SIMPER analysis results showing taxa contributing to 50% of the total similarity within the artificial reef array: (a) with and (b) without translocated *M. modiolus* (n = 12); and (c) dissimilarity between faunal assemblages associated to cultch and sea floor treatments with and without translocated clumps of *M. modiolus*.

a) *M. modiolus* present

Average similarity: 47.27 Species	Average abundance	Average similarity	Contribution %
Pododesmus spp.	2.37	3.02	6.39
Pomatoceros spp.	2.05	2.6	5.49
Modiolus modiolus (spat)	1.75	2.32	4.91
Lyssianasa ceratina	1.89	2.28	4.83
Pisidia longicornis	1.79	2.26	4.78
Hiatella arctica	1.69	2.13	4.5
Balanus balanus	2.27	1.91	4.05
Lepidonotus squamatus	1.31	1.66	3.52
Kefersteinia cirrata	1.48	1.66	3.52
Ascidiella aspersa	1.24	1.34	2.84
Halecium halecinum	1.16	1.31	2.78
Scypha ciliata	1.15	1.3	2.75

b) *M. modiolus* absent

Average similarity: 34.65 Species	Average abundance	Average similarity	Contribution %
Pomatoceros spp.	2.87	5.75	16.58
Balanus balanus	2.3	4.56	13.16
Pododesmus spp.	2.35	4.06	11.71
Pisidia longicornis	1.49	3.14	9.05

c) Effect of translocation

Average dissimilarity = 67.35	*M. modiolus* absent	*M. modiolus* present	
Species	Average abundance	Average abundance	Contribution %
Balanus balanus	2.3	2.27	1.94
Hiatella arctica	0.41	1.69	1.86
Lyssianassa ceratina	0.64	1.89	1.86
Pomatoceros spp.	2.87	2.05	1.77
Cymodoce truncata	0.11	1.32	1.76
Halecium halecinum	0	1.16	1.68
Modiolus modiolus (spat)	0.64	1.75	1.6
Pododesmus spp.	2.35	2.37	1.59
Sertularia spp.	0.27	1.23	1.5

Sertularella polyzonias	0	1.09	1.48
Abra alba	0.45	1.23	1.47
Kefersteinia cirrata	0.57	1.48	1.42
Liljeborgia pallida	0.25	1.18	1.36
Lepidonotus squamatus	0.44	1.31	1.27
Harmothoe impar	0.54	1.12	1.18
Pholoe inornata	0.25	1	1.14
Ascidiella aspersa	0.87	1.24	1.14
Terebellides stroemi	0.93	0.96	1.11
Gibbula cineraria	1.01	0.73	1.11
Polycirrus medusa	0.63	0.97	1.08
Orchomene nana	0.29	0.89	1.07
Ophiothrix fragilis	0.81	0.83	1.06
Brachystomia scalaris	0	0.84	1.06
Hydroides norvegica	0	0.77	1
Nucula nucleus	0.36	0.65	0.99
Corophium sextonae	0.08	0.7	0.99
Scypha ciliata	0.55	1.15	0.98
Spirorbidae	0	0.77	0.92
Musculus costulatus	0.56	0.8	0.91
Eumida sanguinea	0.67	0.79	0.89
Sphenia binghami	0.38	0.64	0.88
Asterias rubens	0.29	0.62	0.88
Flabelligera affiis	0.48	0.67	0.87
Pherusa plumosa	0.43	0.7	0.87
Stylostomun ellipse	0.31	0.59	0.84
Alcyonidium diaphanum	0.28	0.55	0.8
Parvicardium ovale	0.08	0.58	0.8
Pisidia longicornis	1.49	1.79	0.79
Sabellaria spinulosa	0.52	0.46	0.78
Aonides oxycephala	0	0.57	0.78
Capulus ungaricus	0.08	0.55	0.76
Leptochiton asellus	0.17	0.52	0.75
Apseudes talpa	0.08	0.52	0.72

Table 5

Summary of one-way ANOVA analysis of differences in total number of individuals (*N*), species richness (*d*), diversity (*H'*) and evenness (*J*) between natural reefs (n = 10) and artificial reef treatments consisting of translocated *M. modiolus* on cultch (elevated or flattened) or the seafloor (n = 12).

Variable	*SS*	*MS*	*d.f.*	*F*	*P*
N	18.399	4.599	4	19.23	**<0.001**
d	0.0315	0.00789	4	0.19	0.9739
H'	2.3499	0.58747	4	0.46	0.758
J	0.018457	0.004614	4	0.97	0.4508

Significant *P* values are indicated in bold font type (SS = sum of squares; MS = mean square; d.f. = degrees of freedom; *F* = F-ratio).

Table 6

Results of PERMANOVA pair-wise *post hoc* analysis comparing faunal assemblages associated with artificial reef treatments and natural *M. modiolus* beds sampled from Round Island Pinnacle (RIP) and Brown Rocks (BR).

Groups	*t*	*P*	Significance
RIP, BR	1.65	**0.022**	*
RIP, Translocation-Sea floor	2.58	**0.016**	*
RIP, Translocation-Elevated cultch	2.71	**0.014**	*
RIP, Translocation-Flattened cultch	2.86	**0.006**	**
BR, Translocation-Sea floor	2.26	**0.007**	**
BR, Translocation-Elevated cultch	2.19	**0.01**	*
BR, Translocation-Flattened cultch	2.40	**0.011**	*
Translocation-Sea floor, Translocation-Elevated cultch	1.17	0.151	NS
Translocation-Sea floor, Translocation-Elevated cultch	1.19	0.148	NS
Translocation-Elevated cultch Translocation-Flattened cultch	0.93	0.734	NS

Significant *P* values are indicated in bold; asterisks indicate significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS = Not significant.

Table 7

Total numbers of taxa recorded from faunal assemblages associated to *M. modiolus* translocated onto artificial reef treatments constructed in Strangford Lough, Northern Ireland (first row) and natural *M. modiolus* reefs in Europe and North America. Shannon-Weiner's species diversity (*H'*) and Pielou's evenness (*J*) are also included if available (na = data not available).

Location	Taxar	Diversity (*H'*) and Evenness (*J*)	*M. modiolus* reef type (based on Holt et al. 1998)	Sampling method	Source
Artificial reef, Strangford Lough (Northern Ireland, UK)	223	H' = 2.67 - 3.6 J = 0.67 - 0.89	Sublittoral (16 - 20 m)	0.0625 m^2 quadrat removal, hand-collected to 10 cm. One mm mesh sieve	Present study
Strangford Lough, (Northern Ireland, UK)	84	na	Semi-infaunal Sublittoral beds (15 - 20 m)	Dredge and hand collected	Roberts (1975)
Strangford Lough, (Northern Ireland, UK)	90	na	Semi-infaunal Sublittoral beds (15 - 20 m)	Sampling methodology not specified	Brown and Seed (1976)
Strangford Lough, (Northern Ireland, UK)	130-182	H' = 2.5 - 2.8 J = 0.75 - 0.77	Semi-infaunal. Sublittoral beds (15 - 30 m)	0.25 m^2 quadrats removed to 10 cm One mm mesh sieve	Roberts et al. (2004)
Llŷn Peninsula (Wales, UK)	230	H' = 4.77 - 5.40 J = 0.73 - 0.83	Semi-infaunal Sublittoral biogenic reef (25 - 35m)	0.0625 m^2 core samples, air-lift suctioned to 20 cm Hand-picked clumps. 0.5 mm mesh sieve	Rees et al. (2008)
Isle of Man, Irish Sea	270	na	Infaunal Sublittoral biogenic reefs	Unknown	Holt and Shalla (unpublished; reported in Holt et al., 1998 and Rees et al., 2008)
Firth of Lorne, (Scotland, UK)	62	na	Semi-infaunal Sublittoral beds (> 200 m)	Dredge, 1 mm sieve	Collins (1986)
Loch Creran, (Scotland, UK)	80-87 clump[*1]	H' = 4.80 – 5.08., J = 0.76 – 0.81	Semi-infaunal Sublittoral beds (15 m)	Semi-quantitative, 4 replicate hand-picked clumps. 0.5 mm mesh	Mair et al. (2000)

Loch Alsh,)Scotland, UK)	116-90 clump^{-1}	H' = 3.46 – 5.40 J = 0.57 – 0.86	Semi-infaunal Sublittoral beds (20 m)	Semi-quantitative, 4 replicate hand-picked clumps. 0.5 mm mesh sieve	Mair et al. (2000)
Busta Voe, (Shetland, UK)	48-74 clump^{-1}	H' = 3.25 – 4.08 J = 0.57 – 0.72	Semi-infaunal Sublittoral beds (14 m)	Semi-quantitative, 4 replicate hand-picked clumps. 0.5 mm mesh sieve	Mair et al. (2000)
Gulf of St. Lawrence (Canada)	39-46	na	Epifaunal Intertidal populations	0.1 m^2 areas along a transect, dug to 10 cm. Decanting, no sieving	Rowell (1969)
New England (USA)	80	na	Epifaunal Shallow sublittoral	0.25 m^2 quadrats, epifauna removed with knife, air lifted	Witman (1985)
Gulf of Maine (USA)	60	na	Epifaunal Shallow sublittoral	0.25 m^2 quadrats, epifauna removed with knife, air lifted	Ojeda and Dearborn (1989)
Bay of Fundy (Canada)	150	na	Semi-infaunal Sublittoral bioherms (> 100 m)		Fuller (1998) in Kenchington et al. (2006)
Western Bank, off Nova Scotia (Canada)	341	na	Epifaunal Semi-infaunal sublittoral bioherms (> 70m)	0.5 m^2 area sampled to 10 - 25 cm using hydraulic Videograb	Kenchington et al. (2006)

Highlights

- An artificial reef used for restoration of *M.modiolus* communities was investigated.
- The experimental reef consisted of shell cultch and translocated *Modiolus* stocks.
- Cultch offered no significant restoration advantages regardless of elevation.
- *Modiolus* translocation significantly enhanced biodiversity and spat recruitment.
- Species composition was similar in natural and translocated *Modiolus* communities.